Higher heart rate variability is associated with vmPFC activity and increased resistance to temptation in dietary self-control challenges

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Abstract: Higher levels of self-control in decision making have been linked to better psychosocial and physical health. A similar link to health outcomes has been reported for heart rate variability (HRV), a marker of physiological flexibility. Here, we sought to link these two, largely separate, research domains by testing the hypothesis that greater HRV would be associated with better dietary self-control in humans. Specifically, we examined whether total HRV at sedentary rest (measured as the standard deviation of normal-to-normal intervals, SDNN) can serve as a biomarker for the neurophysiological adaptability that putatively underlies self-controlled behavior. We found that HRV explained a significant portion of the individual variability in dietary self-control, with individuals having higher HRV being better able to down-regulate their cravings in the face of taste temptations. Furthermore, HRV was associated with activity patterns in the ventromedial prefrontal cortex (vmPFC), a key node in the brain's valuation and decision circuitry. Specifically, individuals with higher HRV showed both higher overall vmPFC BOLD activity and attenuated taste representations when presented with a dietary self-control challenge. Lastly, the behavioral and neural associations with HRV were consistent across both our stress induction and control experimental conditions. The stability of this association across experimental conditions suggests that HRV may serve as both a readily obtainable and robust biomarker for self-control ability across environmental contexts. SIGNIFICANCE STATEMENT: Self-control is associated with better health, but behavioral and psychometric self-control measures allow only indirect associations with health outcomes and may be distorted by reporting bias. We tested whether resting heart rate variability (HRV), a physiological indicator of psychological and physical health, can predict individual differences in dietary self-control in humans. We found that higher HRV was associated with better self-control and improved predictions of choice behavior. Specifically, higher HRV was associated with more effective down-regulation of taste temptations, and with a diminished neural representation of taste temptations during self-control challenges. Our results suggest that HRV may serve as an easily acquired, non-invasive and low-cost biomarker for self-control ability.

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Higher heart rate variability is associated with vmPFC activity and increased resistance to temptation in dietary self-control challenges

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Abstract

Higher levels of self-control in decision making have been linked to better psychosocial and physical health. A similar link to health outcomes has been reported for heart rate variability (HRV), a marker of physiological flexibility. Here, we sought to link these two, largely separate, research domains by testing the hypothesis that greater HRV would be associated with better dietary self-control in humans. Specifically, we examined whether total HRV at sedentary rest (measured as the standard deviation of normal-to-normal intervals, SDNN) can serve as a biomarker for the neurophysiological adaptability that putatively underlies self-controlled behavior. We found that HRV explained a significant portion of the individual variability in dietary self-control, with individuals having higher HRV being better able to down-regulate their cravings in the face of taste temptations. Furthermore, HRV was associated with activity patterns in the ventromedial prefrontal cortex (vmPFC), a key node in the brain's valuation and decision circuitry. Specifically, individuals with higher HRV showed both higher overall vmPFC BOLD activity and attenuated taste representations when presented with a dietary self-control challenge. Lastly, the behavioral and neural associations with HRV were consistent across both our stress induction and control experimental conditions. The stability of this association across experimental conditions suggests that HRV may serve as both a readily obtainable and robust biomarker for self-control ability across environmental contexts.

Significance statement

Self-control is associated with better health, but behavioral and psychometric self-control measures allow only indirect associations with health outcomes and may be distorted by reporting bias. We tested whether resting heart rate variability (HRV), a physiological indicator of psychological and physical health, can predict individual differences in dietary self-control in humans. We found that higher HRV was associated with better self-control and improved predictions of choice behavior. Specifically, higher HRV was associated with more effective down-regulation of taste temptations, and with a diminished neural representation of taste temptations during self-control challenges. Our results suggest that HRV may serve as an easily acquired, non-invasive and low-cost biomarker for self-control ability.

Introduction

Self-regulation has been associated with a wide range of life outcomes, from educational achievement and socio-economic status to mental and physical health (Mischel et al., 1989; Duckworth, 2011; Moffitt et al., 2011). Therefore, accurate predictors of individuals' self-regulatory abilities are important tools in both basic scientific research as well as applied domains including education and medicine. Self-regulation is generally assessed in specific domains by psychometric questionnaires or laboratory tasks. Unfortunately, participants can potentially distort these measurements by reporting socially desirable answers or behaving according to the presumed goals of the experimenter. Therefore, measures based on physiological readouts that are easy to obtain, domain independent and robust to reporting biases could be an important tool in the assessment of self-control.

One such readout is heart rate variability (HRV). Measures of HRV have been linked to self-regulatory capacities and performance in the domain of emotion (Thayer and Lane, 2000, 2009), raising the question of whether they might serve as more general predictors of self-control. Heart rate variability is a well-established physiological characteristic of all vertebrates (Grossman and Taylor, 2007): the timing between subsequent heartbeats oscillates on the order of milliseconds and no two neighboring beat pairs (RR intervals) are of exactly the same length (Camm et al., 1996). An animal's HRV is sensitive to both physical and mental strain (Porges and Raskin, 1969), and differences in resting HRV can distinguish between states of health and disease (Heni et al., 2014; Heni et al., 2015). High resting HRV has been associated with good physical (Masi et al., 2007; Brandle et al., 2015) and mental health (Thayer and Brosschot, 2005), while

chronic decreases in HRV indicated disease states and slow recovery from stress (Weber et al., 2010; Stalder et al., 2011).

The Polyvagal (Porges, 1995, 2001) and Neurovisceral Integration (Thayer and Lane, 2000, 2009) theories postulate a mechanistic link between HRV and self-regulation. Both associate central nervous system regulation of the cardiovascular system, which is necessary to prepare reactions to challenges in the environment, with adaptive behavior at a higher cognitive level. However, we note that it remains unclear to what degree the central versus peripheral nervous system influences HRV. Despite the fact that we do not yet fully understand all of the physiological and cognitive factors driving HRV (Heathers, 2014), we build on previous proposals (Grossman and Taylor, 2007) and posit that HRV serves as a readout of an individual's allostatic capacities to integrate behavioral strategies and energy stores in response to demands in the environment.

Higher HRV has been linked to several cognitive processes that support self-regulation including: (1) re-allocation of attention (e.g., disengaging from stimuli that are not threatening in the current context), which may reduce allostatic load (McEwen and Wingfield, 2003), (2) persistence (Reynard et al., 2011), and (3) working memory (Gianaros et al., 2004; Hansen et al., 2004). In contrast, low HRV has been associated with disinhibition and dysregulated social conduct (Beauchaine, 2001; Beauchaine et al., 2007). Furthermore, Daly et al. (2014) reported that higher trait self-control, measured using the self-report scale developed by Tangney, Baumeister & Boone (2004), correlates with higher resting HRV. However, the links between HRV and self-control at the neural level remain unknown.

In this study, we investigated the relationship between dietary self-control and resting HRV using fMRI. We hypothesized that better self-control should be associated with higher heart rate variability, and that individual differences in HRV would be associated with neural processing within a self-control network including dlPFC and vmPFC (Hare et al., 2009; Maier et al., 2015). We indeed found that higher resting HRV was associated with better dietary self-control. Furthermore, we found that HRV positively correlated with activity in ventromedial prefrontal cortex (vmPFC) when individuals faced self-control challenges, and that high HRV individuals showed a decreased sensitivity to taste attributes in vmPFC. These vmPFC findings suggest a neural mechanism for the down-regulation of tempting taste attributes that may facilitate dietary self-control.

Materials and Methods

Participants. Fifty-one men participated in this study. The sample is the same as in Maier, Makwana & Hare (2015), where we reported the effects of stress on behavioral and neural self-control processes, but no heart rate analyses. We included only male participants to facilitate the collection and analysis of cortisol responses to stress in our previous work. Baseline HR data for two participants were lost due to recording failure. In the present report, we include the subset of participants for whom we have both heart rate and fMRI data (22 control and 27 stress group participants). The Ethics Committee of the Canton of Zurich approved this study and all participants provided written informed consent on the study day. All participants were right-handed and had normal or corrected to normal vision. None of them reported any history of somatic or psychiatric disease, nor did they

take any prescription medication. On average, participants in the sample had a blood pressure in the (high) normal range for their age group (mean systolic blood pressure: 130 ± 14 SD; mean diastolic blood pressure: 77 ± 9).

Participants were excluded during the recruitment stage if they suffered from any allergies, food intolerances or eating disorders. We also excluded individuals who followed a specific diet (e.g., eating vegetarian, vegan, gluten-/lactose-free, etc.), or who did not report enjoying and regularly consuming snack foods (regularly was defined as more than two occasions per week). A final eligibility criterion was that participants had to report making an effort to maintain a healthy lifestyle, including exercise and an overall balanced diet. Together, these criteria ensured that participants would face a meaningful self-control challenge in the dietary choice task.

To ensure a homogeneous reaction of the hypothalamic-pituitary-adrenal (HPA) axis in response to stress induction, participants were asked to abstain from drinking alcoholic or caffeinated beverages in the 18 hours before the study, to not exercise in the 6 hours prior to the study, and come to the laboratory well rested. We only recruited nonsmokers who had no history of drug abuse. We asked participants to go to bed by 24:00 at the latest on the day before the study and to get a good night's sleep. We instructed participants to not take any medication that alters the blood flow (e.g., analgesics) in the 72 hours before their appointment. In order to motivate the dietary choices, participants were instructed to eat a small meal (sandwich or salad with approximately 450 kcal) 3 hours prior to the study and consume nothing but water after that.

Allen, Chambers & Towers (2007) identified age, exercise habits and obesity as potential confounding factors for heart rate analyses. Our sample was

relatively homogeneous with regard to these factors. The men were 21.2 ± 2 years old, had a normal BMI (Mean: 22.7 ± 2.1 SD), trained on average 1.6 ± 1.4 SD times per week for building strength and had completed an average of 1.9 ± 1.3 SD cardio training sessions per week during the past four weeks before the study, resulting in a combined mean of 3.6 ± 2.1 weekly training sessions per participant. Other factors identified by Allen and colleagues including smoking, gender, caffeine and alcohol intake and circadian rhythm were controlled for by our study exclusion criteria and design.

Procedure. In the 30-40 minutes preceding the resting HRV measurement, participants had rated 180 food items for health and taste in order to create tempting dietary choice pairs. Subsequent to the heart beat interval measurement a stress induction (Socially Evaluated Cold Pressor Test, SECPT) or control procedure was administered. Assignment to the stress induction or control conditions was unknown to both the participant and the experimenter at the time of HRV measurement, however participants knew that they would be randomly assigned to one treatment or the other based on the information provided with the consent forms at the beginning of the study. The SECPT treatment elicited an acute stress response, as indicated by higher cortisol values in the Stress group (mean cortisol in nanomol / liter at maximum: Stress = 9.64 ± 1.09 SEM, Control = 6.6 ± 0.67 SEM), and higher reports of perceiving to be stressed than the Control group (on a visual analog scale from 0, “not at all stressed” to 100, “extremely stressed”: mean Stress = 33 ± 4% SEM, mean Control = 19 ± 5% SEM). Details of the stress induction and behavioral task were reported in Maier et al. (2015). Here, we focus on the relationship between the baseline HRV parameter and dietary self-control

success and its neural correlates. However, given that the stress treatment is known to change dietary choices (Maier et al., 2015), we included it as a factor in all regression models.

Immediately after the stress induction, participants were scanned with BOLD fMRI while they made choices in a dietary self-control task. The screen always depicted two food items, and participants had to choose whether they wanted to eat the item on the right or on the left (Figure 1a). The binary food choices fell into one of two categories. In the first, choosing the healthier item is trivial because the healthier item was also tastier. We refer to this category as no challenge trials because there is no self-control challenge. In the second choice category, self-control challenges, the healthier item was the less tasty of the two foods and thus presented a conflict between taste and health attributes. Self-control challenges were presented on approximately half of the 210 trials for each participant. To examine the variability of the challenge that different participants faced, we normalized the ratings to fall between 0 and 100 points, and calculated absolute taste and health differences between every pair of food items each participant faced. On a scale from 0 to 100, the mean health difference was 34 ± 25 points (mean ± standard deviation) and the mean taste difference was 29 ± 21 points.

The behavioral and fMRI analyses in this paper focus on the self-control challenge cases. Before the task started, they were reminded to choose the healthier item as often as they could, consistent with their healthy lifestyle goals. Participants knew that one of their choices would be realized in the end, and they would have to eat whatever they chose on the trial that was randomly drawn for being paid out.

Psychometric inventories. German versions of the Spielberger State-Trait Anxiety Inventory (Laux et al., 1981), Three Factor Eating Questionnaire (Pudel and Westenhöfer, 1989), and Behavioral Inhibition and Activation Scales (Strobel et al., 2001) were administered at the end of the study. Data for the trait anxiety scale of the State-Trait Anxiety Inventory are missing for one participant, as he failed to complete the second page of the questionnaire.

Statistical Analyses. All behavioral data were analyzed using either the Matlab (Release 2014b, version 8.4.0.150421 (The MathWorks Inc., 2014), RRID:SCR_001622) or R (Version 3.2.1 ("R Core Team," 2015), RRID:SCR_001905) statistical software packages. The fMRI results were depicted using the MRIcron software package (http://www.mccauslandcenter.sc.edu/mricro/mricron/, RRID:SCR_002403). All correlations reported in this paper were assessed with a nonparametric bootstrap method. Two-tailed p-values for correlations were obtained by testing the Pearson correlation coefficients (r) against a null distribution generated from 5000 permutations of the data. The 95 % confidence intervals for the correlations were computed from 5000 bootstrapped samples of the data. The multiple regression model in equation 2 below was fit using the "lm" function in R. In order to visualize the HRV by taste and health difference interactions, we plot the estimated self-control success levels at specific combinations of HRV and taste or health differences from this regression model (Figure 2b and c).

Heart rate data acquisition. We measured baseline heart rate (HR) at rest with the Polar RS 800 CX system (for a cross-validation of this method with ECG see Quintana, Heathers & Kemp (2012)). All measurements were collected between 13.30 and 17.00 in the afternoon to control for circadian rhythms (Heathers, 2014). The baseline measurement was always taken in a single session before any stress or control treatment was administered. Participants were seated in a quiet room and instructed that upon mounting the Polar watch and pressing start, they would need to sit upright and remain quiet and calm during the subsequent baseline-recording interval. A baseline recording was taken for 6 minutes. The first 3 minutes of the recording were discarded from the analysis to yield a set of data that were less affected by aspects such as initial motion while acclimatizing to the recording environment (Quintana et al., 2016). We focused on baseline (i.e. resting) heart rate measures in order to obtain a domain-general index of HRV.

Heart rate data analyses. HRV can be calculated in two different domains: time and frequency. The full range of measures is discussed in the guidelines by the Task Force on HRV (Camm et al., 1996). Time domain measures have the advantage of being more robust than frequency measures. Two different time domain measures are commonly used and both characterize the distribution of inter-beat intervals, which are defined as the time between two subsequent heart beats (i.e., the difference between two R peaks in the ECG (Guyton and Hall, 2006), hence also called the "RR interval"; see Figure 1b). The standard deviation of all RR (also "NN" for "normal-to-normal") intervals, SDNN, describes the total heart rate variability within a given period (see equation 1). The root mean square of successive differences (RMSSD) calculated between adjacent RR intervals is more

sensitive to influences of short-term regulation of the heartbeat. Here we focus on HRV at rest (i.e. in the absence of specific, discrete input stimuli), and thus take SDNN as our primary measure of variability.

We chose total HRV (measured as standard deviation over all RR intervals, SDNN) as our biomarker for two reasons: First, SDNN is deemed to be the most robust measure of HRV. Among all commonly computed HRV measures it has been reported to be least compromised by different data preprocessing pipelines, especially the application of artifact correction (Salo et al., 2001). Second, the process of dietary choice is a complex behavioral outcome that may not only depend on a capacity for effective cognitive regulation that helps to achieve self-control goals, but may also be influenced by peripheral factors (e.g., endocrine status, metabolism and energy expenditure) that are indicative of the current state of the organism. SDNN reflects all influences on the RR interval series, while it is known to correlate highly, although not perfectly, with measures that putatively reflect phasic vagal control of cardiac variability in measures taken under sedentary resting conditions (Allen et al., 2007).

The complete recording of RR intervals for each participant was extracted using the Polar software, without any transformations of the data. Three-minute intervals of the raw data were then pre-processed with the Artiifact toolbox (Version 2.08, 64-bit, Kaufmann et al. (2011)), which has a better artifact detection rate and shows less false detections than the commonly used Kubios HRV toolbox. The Artiifact toolbox implements the algorithm of Berntson & Stowell (1998) for identifying artifacts, which aims to exclude any potential artifacts before computing the criterion for identifying true artifacts. Based on the report of Salo and colleagues (2001), who compared editing procedures for correcting single RR

artifacts, the identified artifacts were deleted from the RR sequence to obtain the cleanest estimate for SDNN. On average, we corrected 2.1 ± 3.1 SD % of the RR intervals in each sample. Apart from two datasets that had a high number of artifacts requiring correction (12.6 % and 10.5 % RR intervals removed), all other datasets had between 0 and 6% artifacts corrected (21 datasets were diagnosed as being completely artifact free). As a high number of corrected artifacts might be a concern for interpreting our findings, we checked all models for robustness with regard to the number of corrected artifacts.

SDNN was calculated as

(1)

$$SDNN = \sqrt{\frac{1}{N-1}\sum_{j=1}^{N}\left(RR_j - \overline{RR}\right)^2}$$

Heart rate variability was calculated with the Artiifact software suite, using Fast Fourier Transforms (Berntson and Stowell, 1998; Kaufmann et al., 2011) with an interpolation rate of 4 Hz (spline interpolation) and a Hanning window width that matched the total length of the edited recording (max. 180 seconds or slightly less in case of deletion correction). Frequency bands were bounded between 0.003 and 0.04 Hz for the very low frequency band, 0.04 and 0.15 Hz for the low frequency band, and 0.15 and 0.4 Hz for the high frequency band.

fMRI data acquisition. Images were acquired using a Philips Achieva 3 T whole-body scanner with an eight-channel sensitivity-encoding head coil (Philips Medical

Systems) at the Laboratory for Social and Neural Systems Research, University Hospital Zurich. Stimulus presentation was controlled with the Psychophysics Toolbox Software (Psychtoolbox 3.0, Brainard (1997), RRID:SCR_002881); the paradigm was presented via a back-projection system to a mirror that was mounted on the head-coil.

We acquired gradient echo T2*-weighted echo-planar images (EPIs) with blood-oxygen-level-dependent (BOLD) contrast (41 slices per volume, Field of View 200 x 126.5 x 200 mm, slice thickness 2.5 mm, 0.6 mm gap, in-plane resolution 2.5*2.5 mm, matrix 80*80, repetition time 2460 ms, echo time 30 ms, flip angle 77°) and a SENSE reduction (i.e. acceleration) factor of 2. Volumes were acquired in axial orientation at a +15° tilt to the anterior commissure-posterior commissure line. We collected 161 volumes in ascending order during each of the three experimental runs, together with five "dummy" volumes at the start and end of each run. A T1-weighted turbo field echo structural image was acquired in sagittal orientation for each participant at the end of the scanning session with the same angulation that applied to the functional scans (181 slices, Field of View 256 x 256 x 181 mm, slice thickness 1 mm, no gap, in-plane resolution 1*1 mm, matrix 256*256, repetition time 8.4 ms, echo time 3.89 ms, flip angle 8°). To measure the homogeneity of the magnetic field we collected B0/B1 maps before the first and second run and before acquiring the structural scan (short echo time = 4.29 ms, long echo time = 7.4 ms). We measured breathing frequency and took an electrocardiogram with the in-built system of the scanner in order to correct for physiological noise.

fMRI Preprocessing. Functional data were spatially realigned and unwarped with statistical parametric mapping software (SPM8, Update Rev. Nr. 5236; Functional

Imaging Laboratory, University College London, RRID:SCR_007037), segmented according to the participant's T1-weighted high resolution structural image and normalized to the individual mean EPI template before smoothing with an isometric Gaussian kernel (4 mm full width at half maximum). As a last step in preprocessing, we used RETROICOR, as implemented in the PhysIO toolbox, to model respiration and heartbeat (Glover et al., 2000) in order to account for fluctuations in the BOLD signal due to physiological noise. The PhysIO Toolbox by Kasper (2009) is distributed as open source code as part of the TAPAS software collection: www.translationalneuromodeling.org/tapas/. Following Harvey et al. (2008), its algorithm uses Fourier expansions of different order to the estimate the phases of cardiac pulsation (3rd order), respiration (4th order) and cardio-respiratory interactions (1st order). For two participants, the scanner could not save physiological data due to a technical problem. For these participants, only the standard motion correction procedure was applied.

fMRI analyses

General linear models. In all fMRI analyses, regressors in the models were defined as boxcar functions with durations equal to the reaction time on each trial. All three fMRI models also included regressors for head motion, respiratory and cardiac effects on each trial to account for variance in the BOLD signal associated with these sources of noise.

Our primary general linear model (GLM-CH) tested for regions that correlated with HRV during self-control challenges (CH). The regression modeled as events of interest all trials that contained 1) a challenge, 2) no challenge, while controlling for 3) healthier experimenter recommendations and 4) less healthy

experimenter recommendations. Note that the experimenter recommendations were included in the choice task to test a separate hypothesis unrelated to the current report and are not discussed here. Self-control challenge and no challenge trials included parametric modulators for relative health and taste differences. We computed a first-level contrast for Challenge > No Challenge trials. At the second (group) level, we examined whether increases in BOLD activity on challenge trials were correlated with HRV levels using non-parametric permutation tests (n = 5000 permutations) and included threshold-free cluster enhancement (TFCE) as implemented in the function "Randomise" in the fMRIB Software library (FSL 5, FMRIB, Winkler, Ridgway, Webster, Smith & Nichols (2014), RRID:SCR_002823). We used FSL for the group level analyses because the TFCE and permutation algorithms are more fully documented and run considerably faster in FSL compared to their implementation in SPM12.

A second, separate GLM (GLM-SV) was computed to determine if BOLD activity was related to the integrated value of the chosen food. This GLM included parametric regressors for the integrated subjective value of the chosen and non-chosen food items on every choice onset. Once again, additional regressors controlling for the impact of the experimenter recommendations were included in the model with separate regressors for events in which participants chose based on the recommendation, and in which they did not follow the recommendation. We modeled each participant's subjective value of food items on every trial by combining the weighted values for the taste and health of each food. The weights were derived from individual logistic regressions on the participant's choices (identical to Maier et al. (2015)). Briefly, for each participant, a logistic regression estimating the probability of choosing the left item as a function of the taste and

health of the left and right item, with all ratings z-scored within participant before entering them in the model. Two additional binary regressors indicated whether the left or right item had been recommended. These regressors for left and right item recommendations took the value of 1 when the item was recommended, and 0 when it was not recommended. When no recommendation was given on a trial, both regressors had a value of zero. Note that the spatial presentation of the items was completely randomized, so that the left item was equally likely to be the healthier, or the tastier of both options. We took the mean of the taste betas for the left and right item obtained for each participant, averaging them into a common taste weight for this individual. The same was done for health. These averaged taste and health weights were then used to multiply the z-scored taste and health values of each item presented in the choice paradigm. To obtain the subjective value for each food, the weighted taste and health values were added up to a weighted subjective value separately for the left and right food items.

We computed a first-level contrast for the chosen food value for each participant and extracted betas from this contrast within our functional ROI of the ventromedial prefrontal cortex (vmPFC).

To examine the impact of health and taste attributes on the BOLD signal, we used a third GLM that modeled five events: 1) all choices, 2) trials on which the healthier food was recommended and chosen, 3) trials on which the healthier food was recommended and not chosen, 4) trials on which the less healthy food was recommended and chosen, and 5) trials on which the less healthy food was recommended and not chosen. Note that the 30 baseline trials did not contain any recommendation, and therefore, the sum of regressors 2-5 does not equal regressor 1. The first regressor for all choices included four parametric

modulators: 1) health of the chosen item (Hc), 2) taste of the chosen item (Tc), 3) health of the non-chosen item (Hnc), and 4) taste of non-chosen item (Tnc). These parametric regressors were not orthogonalized with respect to one another. We computed first-level contrasts for Tc-Tnc and Hc-Hnc. We then extracted the betas for these contrasts from our functional vmPFC ROI. The significance of the correlations between BOLD sensitivity to taste and health differences in vmPFC and HRV were determined from 5000 permutations of the data.

Anatomical masks. The combined anatomical mask for the vmPFC was constructed from a conjunction of the bilateral frontal pole, frontal medial, paracingulate and subcallosal cortex areas that exceeded 20% probability of belonging to the respective structure in the Harvard-Oxford Cortical Atlas (HOA; Desikan et al. (2006)). In order to limit the mask to our region of interest along the medial wall, the HOA-derived anatomical mask was intersected with a rectangular box around the midline (coordinates in mm : x = [- 22, 21], y = [-110, 73], z = [-35, 9]).

The anatomical mask of the left dlPFC was constructed from a conjunction of the left inferior frontal gyrus (pars opercularis and reticularis) and left superior frontal gyrus areas that exceeded 20% probability of belonging to these structures according to the HOA.

Because we tested two separate regions of interest (vmPFC and dlPFC), we used a critical value of $p < 0.025$ (i.e. 0.05 / 2) for small volume correction at the voxel-level.

Health, taste, and appetitiveness ratings. Participants rated health, taste, and how appetizing they found the depicted foods on a continuous rating scale with

anchor points from -5 for "very untasty / unhealthy" to +5 for "very tasty / healthy", or vice versa, to counterbalance order effects. Taste and health ratings were not correlated: the median correlation was -0.09 ± 0.31 MAD in the Stress group, and -0.06 ± 0.20 MAD in the Control group. Neither health ($r = -0.12$, $p = 0.40$), nor taste ($r = 0.09$, $p = 0.56$), nor appetitiveness ratings ($r = 0.13$, $p = 0.37$) were correlated with hunger levels.

Results

HRV. The mean duration of RR intervals across all participants was 929.3 ± 136.3 ms (sample median of the median duration of RR intervals: 947 ± 115 ms), resulting in a mean heart rate of 66 ± 10 beats per minute in our sample (values are derived after deletion of artifacts). Our participants expressed a median total HRV (measured as standard deviation over all RR intervals, SDNN) of 98.7 ± 30.1 ms median absolute deviation (MAD) within our 3-minute baseline measurement. Consistent with previous reports (Tsuji et al., 1996), HRV was inversely related to average heart rate (beta = -1.17 +- 0.47, T = -2.48, $p = 0.017$; see Table 2). However, total HRV did not differ between participants later assigned to the Stress (S) or Control (C) groups (S: 98.7 ± 29.6 ms; C: 97.7 ± 30.9 ms, $p = 0.93$, $Z = 0.09$, Wilcoxon rank sum test). Regarding biological and psychological markers of the stress reaction, baseline SDNN and cortisol reactions (area under the curve with respect to ground (Pruessner et al., 2003)) were not significantly correlated ($r = -0.19$, $p = 0.18$), nor were baseline SDNN and perceived stress ($r = -0.10$, $p = 0.49$). Visual inspection of a scatter plot revealed one outlier in the SDNN measure: The value for this participant fell between two and three standard deviations from the

463 sample mean. Therefore, we checked our results for robustness with and without
464 this participant's data and found that all results remained significant in both cases.
465 One concern in the evaluation of heart rate variability is that applying artifact
466 correction might inflate indices of HRV (Heathers, 2014; Quintana and Heathers,
467 2014) and as little as one edited artifact in the RR interval series may do so
468 (Berntson and Stowell, 1998). Indeed, we observed a significant positive
469 correlation between the number of artifacts that we corrected per dataset and the
470 SDNN ($r = 0.44$, $p = 0.003$, CI [0.26, 0.61]). Thus, we included the number of
471 corrected artifacts and mean heart rate as additional covariates in our regression
472 model to test whether HRV would be predictive beyond these influences.
473
474 ***HRV and self-control behavior.*** We originally defined self-control success as
475 choosing the healthier, but less tasty of two food items in challenging trials in
476 which health and taste conflicted, meaning that the participant had to overcome
477 his own taste preferences in order to choose the healthier option. We initially
478 tested the relationship between total HRV (i.e. SDNN) and self-control success in a
479 bivariate correlation analysis. Total HRV was associated with the frequency of self-
480 control success in the dietary choice task over all participants (Pearson $r = 0.36$, p
481 $= 0.01$, CI = [0.07, 0.59]; all p values are derived from 5000 permutations of the
482 data; excluding the HRV outlier: $r = 0.33$, $p = 0.02$, CI = [0.03, 0.58]). For
483 comparison, the correlation between self-control success and the cognitive
484 restraint in eating score (RE) obtained from the Three Factor Eating Questionnaire
485 (Pudel and Westenhöfer, 1989) was $r = 0.35$ ($p = 0.01$, CI = [0.11, 0.55]). This
486 restraint score captures the degree to which individuals use cognitive strategies to
487 limit calorie intake, for example by counting calories, deliberately picking small

488 portions of food, or consuming foods with lower calorie content. Thus, as a
489 biomarker of dietary self-control, HRV explains roughly the same amount of
490 individual variance in choice behavior as an established psychometric index of
491 eating behavior. Restrained eating scores were not significantly associated with
492 HRV ($r = 0.14$, $p = 0.35$, CI = [-0.28, 0.42]), suggesting that the two measures could
493 be readily combined to explain additional variation in self-control behavior.

494 Therefore, we modeled self-control success (i.e., choosing a healthier, less
495 tasty item; SCS) in a multiple regression that included both HRV and RE together
496 (see Eq. 2). Beyond testing whether or not HRV and RE could be combined to
497 explain additional variance in self-control, we included RE in the model because it
498 is a widely used, validated measure for dietary self-control success (Laessle et al.,
499 1989; Allison et al., 1992; Williamson et al., 2007). As such, it serves as a
500 benchmark for judging the utility of HRV as a biomarker for dietary self-control.
501 When including both RE and HRV into the same model, we can assess whether
502 HRV is predictive beyond a known trait characteristic of dietary self-control
503 success.

504

505 (2) SCS = (Stress + HRV + RE) * (Hdiff + Tdiff) + error

506

507 This regression allowed us to examine potential interactions between the
508 individual characteristics of HRV and RE and task features such as the stress
509 manipulation (Stress) as well as the average health (Hdiff) and taste differences
510 (Tdiff) a participant faced within the food choice task. Note that although all
511 participants faced self-control challenges in the food choice task, the degree of the

512 challenges depended on each individual's opinions on the taste and healthiness of
513 the various foods.

514 Higher HRV and RE characteristics reduced the influence of taste
515 temptations in self-control dilemmas. All results from the regression in equation 2
516 are listed in Table 1. Higher HRV levels increased the degree to which high taste
517 temptations (i.e. taste differences) were overcome, leading to greater self-control
518 success (Figure 2b). Moreover, unlike low HRV participants, those with high HRV
519 successfully employed self-control regardless of the average health difference
520 between the two options suggesting that they engaged self-control even when the
521 benefit of doing so (i.e. the increase in healthiness) was relatively small (Fig. 2c). A
522 similar interaction was observed between RE and taste differences. As previously
523 reported (Maier et al., 2015), acute stress reduced the use of self-control in dietary
524 choice. To determine if HRV could act as a buffer against acute stress, we computed
525 an extended version of the model in Eq. 2 that also included interactions between
526 stress and HRV and RE. However, we did not observe significant interactions
527 between Stress and HRV or RE indicating that the relationship between HRV and
528 dietary self-control persisted in both in the Stress and Control groups, but that
529 HRV was not associated with resilience to acute stress. For simplicity and ease of
530 interpretation we report the reduced model without interaction terms in Table 1.

531 As a robustness check, we controlled for the influences of the HRV outlier
532 and several other factors that might relate to HRV. We estimated the basic model
533 (equation (2)) without the HRV outlier, and adding: age, the combined number of
534 cardio and strength exercise sessions per week, BMI, hunger level, trait anxiety
535 score, mean heart rate, and number of corrected artifacts in the recording as
536 nuisance regressors. The results were qualitatively unchanged and we still

observed a significant relationship between taste and HRV as described above ($T = 4.77$, $p = 4.85e\text{-}05$). Note that we included trait anxiety in this robustness check because previous work has shown that trait anxiety is also correlated with HRV (Gaburro et al., 2011; Verkuil et al., 2014), and therefore we tested for this relationship in our data as well. We used the trait scale of the Spielberger State-Trait Anxiety Inventory as our measure of anxiety (Median score for our sample: 34.5 ± 5.9 out of possible score ranging from 20-80). Consistent with previous reports, we observed a negative correlation between HRV and trait anxiety scores (permutation $r = -0.28$, $p = 0.0488$, CI [-0.48, -0.06]). Trait anxiety scores were also positively correlated with mean resting heart rates across participants ($r = 0.39$, $p = 0.01$, CI [0.11, 0.60]).

In order to assess the predictive qualities of RE and HRV with regard to self-control in a more robust way, we predicted self-control levels out-of-sample using the leave-one-subject-out (LOSO) method. After taking one participant's data out of the sample, we fit the model in equation (2) to explain the variance in self-control levels of the remaining participants. Using the beta coefficients from the training set, we then predicted the self-control level of the left-out participant. Squaring the obtained correlation coefficient for the true and predicted self-control levels in the full model ($r = 0.88$, $p < 0.0001$, CI = [0.81, 0.92]) yielded the coefficient of determination for the model with combined predictors of RE and HRV, $R^2 = 0.77$ (Figure 2a). For comparison, fitting the model without the predictors for HRV and its interactions yielded a lower correlation between true and predicted self-control levels ($r = 0.81$, $p < 0.0001$, CI = [0.63, 0.88]), leading to an observed $R^2 = 0.65$. That is, by combining RE and HRV, we were able to significantly explain an extra 12% of the variation in out-of-sample self-control

rates. Using a "split half" instead of a LOSO procedure (i.e. randomly sampling half the dataset for model fitting and using the remaining half for predicting out of sample) yielded a similar benefit (16%) for including HRV in the predictive model (full model: $r = 0.81$, $p < 0.0001$, CI = [0.55, 0.92], $R^2 = 0.66$; model without HRV: $r = 0.71$, $p = 0.0004$, CI = [0.26, 0.89], $R^2 = 0.50$).

During the initial review of this manuscript an anonymous reviewer made the insightful suggestion that we could also test the relationship between HRV and another form of self-control in our dataset. Our food choice paradigm included recommendations about which food to choose, and in some cases these recommendations were in favor of the unhealthy food (Participants were told that recommendations were usually, but not always in favor of the healthier item). This feature allows us to test whether HRV is associated with the fraction of trials in which participants overrode this unhealthy recommendation and still chose the healthier food. We found that there was also a positive correlation between HRV and this alternative measure of control ($r = 0.31$; $p = 0.01$, CI: [0.01, 0.56]). Although these two measures of self-control are not independent because both are based, in part, on the incorporation of health attributes into the choice process (correlation between self-control measures: $r= 0.77$, $p < 0.0001$, CI: [0.62 0.87]), this post-hoc finding is consistent with the idea that HRV is a domain general marker of self-regulatory ability or efficiency as outlined in the introduction section.

HRV and BOLD activity during self-control. To investigate whether HRV could serve as a biomarker of changes in the brain's decision circuitry in the food self-control paradigm, we analyzed blood oxygenation level-dependent (BOLD) activity

587 measured during the choice task. Our primary general linear model (GLM-CH)
588 tested for regions that correlated with HRV during self-control challenges (CH).
589 Heart rate variability positively correlated with self-control at the level of
590 observed choices, and therefore, we hypothesized that HRV would be associated
591 with BOLD activity in regions known to be involved in the value computation
592 process during self-controlled choices, namely the vmPFC and dlPFC. We tested
593 this hypothesis in anatomical masks of the vmPFC and dlPFC based on the
594 Harvard-Oxford Cortical Atlas (Desikan et al., 2006). The vmPFC mask comprised
595 the bilateral ventromedial prefrontal cortex that is part of the brain's valuation
596 system (Bartra et al., 2013; Clithero and Rangel, 2014; Abitbol et al., 2015;
597 Pessiglione and Delgado, 2015) and has been shown to integrate taste and health
598 values in the dietary self-control paradigm (Hare et al., 2009; Hare et al., 2011;
599 Hare et al., 2014; Foerde et al., 2015; Maier et al., 2015) as well as the separate
600 characteristics of multi-attribute choices in other, non-food domains (Kahnt et al.,
601 2010; Rudorf and Hare, 2014). Our second anatomical mask included the region of
602 left dlPFC that has been presumed to modulate activity in the vmPFC during self-
603 control choices (Hare et al., 2009; Hare et al., 2011; Hare et al., 2014). We found
604 that BOLD activity in portions of the vmPFC increased as a function of baseline
605 HRV in Challenge > No Challenge trials (MNI peak: [1 46 0] in the paracingulate /
606 cingulate gyrus, small-volume-corrected (SVC) $p = 0.004$, $T = 4.8$, and a separate,
607 more dorsal cluster in the cingulate gyrus at [21 41 9], SVC $p = 0.038$, $T = 3.86$; see
608 Figure 3a). However, we found no association between HRV and BOLD activity in
609 the left dlPFC for the Challenge > No Challenge trials that survived small-volume
610 correction within the anatomical region of left dlPFC. Exploratory whole-brain
611 analyses yielded no other regions that survived correcting for multiple

comparisons. The results of these exploratory analyses can be accessed in a Neurovault repository under the following link: http://www.neurovault.org/collections/DNXFVQPJ/.

To establish that activity in this vmPFC region (the larger cluster with a peak at xyz = 1 46 0) was relevant to the participants' choices, we tested whether the chosen food values were represented in the functional ROI correlating with HRV. An integrated value of the chosen food was calculated in a separate GLM (GLM-SV) and we extracted the betas for this chosen food value in the vmPFC ROI. We found that activity in this ROI encoded the integrated value of the chosen food ($T_{46} = 3.52$; $p < 0.001$).

Given our behavioral data linking HRV to the relative influence of taste on dietary choices, we tested whether HRV was also correlated with the degree to which BOLD activity in the vmPFC ROI represented taste attributes (Taste chosen – nonchosen from GLM-HT). We found that HRV was negatively correlated with the relative taste value representation (Pearson r = -0.42, p = 0.002, CI = [-0.60, -0.19]; see Figure 3b), but not correlated with the relative health value (r = - 0.12, p = 0.42, CI = [-0.43, 0.21], Figure 3c). Excluding the HRV outlier did not change the results (taste r = -0.43, p = 0.004, CI = [-0.63, -0.17]; health r = -0.09, p = 0.56, CI = [-0.43, 0.23]).

Discussion

We found that higher HRV is associated with better self-control in the face of dietary challenges. More specifically, our results show that the choices of individuals with higher HRV are less affected by tempting taste attributes than choices of participants with lower HRV. In parallel, at the neural level, higher HRV

correlated with a decreased representation of taste attributes in vmPFC, a brain region that has been associated with both regulating autonomic responses (Benarroch, 1993) and calculating subjective values of choice options (Bartra et al., 2013; Clithero and Rangel, 2014; Abitbol et al., 2015; Pessiglione and Delgado, 2015). Heart rate variability is a measure of physiological fitness that relates to the integrated functioning of the nervous and cardiac systems. Similarly, successful self-control (SC) relies on the integration, and potentially modified evaluation, of actions in the context of higher order goal attainment. Our data indicate a significant association between these integration processes at the basic physiological (i.e. HRV) and cognitive (i.e. SC) levels, suggesting that HRV measures may serve as a useful and readily obtainable biomarker for self-control abilities.

Resting HRV measured over a few minutes with relatively inexpensive and commercially available equipment predicted subsequent self-control in a dietary choice task as well as a validated psychometric index of dietary behavior (restrained eating scale of the Three Factor Eating Questionnaire, RE). Moreover, as a physiological measure that is presumably outside the domain of conscious control, HRV also has the advantage of being immune to socially desirable reporting (Logan et al., 2008; DeVylder and Hilimire, 2015) or memory errors that can affect the accuracy of self-reports. However, when entered into a joint model, both HRV and RE were significantly related to dietary self-control suggesting that they explained separate components of the variance in dietary choice. Thus, it is possible to combine biomarkers such as HRV with behavioral and self-report measures (e.g. the Three Factor Eating Questionnaire) to predict future self-control more accurately.

661 The fact that biomarkers such as HRV can be easily acquired and readily
662 combined with other survey or task-based measures of self-control is important
663 because, taken in isolation, any single measure is likely to reveal only a partial
664 picture of self-control abilities or proclivities. In a recent meta-analysis by
665 Duckworth and Kern (2011), informant-report and self-report questionnaires,
666 behavioral readouts of executive function and delay of gratification measures
667 showed only moderate convergent validity. In other words, self-control assessed in
668 one fashion was only moderately related to self-control measured in another
669 manner. In agreement with those authors, we believe that self-control is a
670 multidimensional construct that is best assessed, and potentially forecasted, by
671 combining measures taken across multiple domains including behavior, self and
672 informant report, and both neural and more general physiological markers such as
673 HRV.

674 Heart rate variability can explain individual differences in self-control that
675 are robust to changes in environmental context. We have previously shown that
676 experiencing an acute stressor results in diminished self-control in the 45-minute
677 period following stressor onset (Maier et al., 2015). In the same sample, we find
678 that resting HRV before stressor onset predicts the level of self-control following
679 stress as well as it predicts choice in the control (i.e. not stressed) participants.
680 Thus, the association between HRV and self-controlled behavior is maintained
681 under the influence of acute stress, suggesting that the association between HRV
682 and self-control may be context independent.

683 Our current findings linking resting HRV to subsequent self-control
684 performance extend previous work reporting correlations between HRV and
685 neural activity measured simultaneously during affective and cognitive tasks. In a

686 study using Positron Emission Tomography and an emotion task, Lane et al.
687 (2009) measured regional cerebral blood flow (rCBF) when participants immersed
688 themselves during 1 minute-blocks into positive, negative, and neutral emotions
689 (evoked by film clips and vignettes of personal emotional memories) while parallel
690 PET and HRV were recorded. During the presentation of emotional (versus
691 neutral) stimuli, HRV correlated with rCBF in the caudate, midbrain, left insula,
692 and medial prefrontal cortex. When excluding all emotion-specific activation, HRV
693 correlated with rCBF in the right dorsolateral prefrontal cortex (dlPFC), bilateral
694 parietal cortex, and the left rostral anterior cingulate cortex (ACC) with high-
695 frequency (parasympathetic) components of HRV. Similarly, Gianaros et al. (2004)
696 used PET to correlate HRV with changes in rCBF in medial orbitofrontal cortex
697 (OFC), insula, ACC, amygdala, hippocampus and cerebellum as a function of task
698 demand in a working memory paradigm. A study by Nugent, Bain, Thayer, Sollers
699 & Drevets (2011) found HRV to be correlated with rCBF in lateral and medial OFC
700 when participants had to achieve different levels of strength in a handgrip task.

701 In contrast to Lane and colleagues' (2009) emotion task results and our *a*
702 *priori* predictions, we did not observe any significant correlations between HRV
703 and activity in the dlPFC during dietary choices. However, the differences in HRV
704 indices and measurement times (resting vs. task) preclude direct comparisons
705 between the previous emotion regulation and current dietary self-control results.
706 It is possible that HRV measures collected during the self-control task would tie in
707 more closely with regulation processes in dlPFC. However, our goal in the current
708 study was to test whether simple, task-independent measures of HRV are
709 associated with dietary self-control. What is consistent across studies is that
710 individual differences in HRV are correlated with activity in neural regions linked

to task performance across several domains (e.g. emotion regulation, working memory, physical effort and dietary self-control). Together these results indicate that efforts to link cognition with central and peripheral neurophysiology may promote a better understanding of the nature of individual differences in health and cognitive behaviors, and provide opportunities for prediction and early intervention against dysfunctions (see for example Sokol-Hessner et al. (2009) and Raio et al. (2013)).

Our study represents an important initial step in linking total HRV to self-control ability. This result suggests total HRV should be considered when investigating links between self-control and allostatic capacity in addition to more direct indices of phasic vagal cardiac control of HRV, such as RMSSD and high-frequency HRV. One rationale for doing so in the domain of dietary self-control is that frequency components outside the high-frequency spectrum may include information on metabolic and endocrine processes that are directly relevant to dietary decisions. These components contribute to the total HRV, but oscillate on a slower time scale (Berntson et al., 1997).

Further progress could be made by addressing this question with causal manipulations, for example by inducing endocrine signals of hunger and satiety and investigating whether the association between total HRV and self-control success varies during these states. Another interesting avenue to pursue is whether plasticity-induced changes that enable better regulation, for example through transcranial electrical or magnetic stimulation of the dlPFC, might also lead to an increase in HRV. A study in autistic children suggests this might be the case: Wang et al. (2015) found that weekly treatment with low-frequency repetitive transcranial magnetic stimulation (rTMS) for 3 months both improved

chronic autonomic imbalance (i.e., higher low frequency and lower high-frequency contributions to total HRV, putatively reflecting a tonically high arousal level due to activation of the sympathetic nervous system) and reduced the tonically elevated skin conductance levels commonly seen in autism. This change was accompanied by decreased irritability, hyperactivity, and less stereotyped and compulsive behavior in the autistic children. Future work could therefore address this regulatory mechanism in a healthy population with a similar causal manipulation by stimulation techniques to further explore the nature of the link between neural correlates of self-regulation and physiological markers of allostatic capacity.

In conclusion, heart rate variability is a marker of cardiovascular and mental health. Our results indicate that heart rate variability also explains significant variation in self-control during dietary choice. Moreover, both HRV and a standard psychometric scale of restrained eating contributed independently to explaining variance in our behavioral model of self-control and could be used in combination to better predict dietary self-control levels.

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Conflict of interest

The authors declare no competing financial interests.

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959

960 **Figure Legends**

961 **Figure 1.** Behavioral and physiological measurements. **(a)** In the dietary self-
962 control task, participants made a series of choices between two items on the
963 screen, that represented items they would eat at the end of the study. In the
964 challenge trials that are the focus of this paper, choosing the healthier food
965 required forgoing the tastier option. **(b)** This stylized sketch highlights the R peaks
966 of the ECG curve. The RR interval describes the distance between two subsequent
967 R peaks. In the healthy heart, the length of subsequent RR intervals consistently
968 differs on the order of milliseconds, which allows calculating heart rate variability
969 characteristics.

970

971 **Figure 2.** Combining behavioral and heart-rate variability measures to predict
972 self-control success rates. HRV and restrained eating trait (RE) were uncorrelated
973 and predicted independent and significant portions of the variation in self-control
974 behavior in our combined behavioral model (see Table 1). **(a)** This scatter plot
975 shows the association between predicted and observed self-control (SC) success
976 rates. We used the model listed in equation 2 together with a "Leave One Subject
977 Out" (LOSO) procedure to predict self-control success. Including the predictors for
978 baseline HRV and its interactions with taste and health aspects yielded a
979 coefficient of determination $R^2 = 0.77$. Moreover, omitting HRV from the predictive
980 model resulted in a 12% decrease in explained variance. The error bar plots in
981 panels b and c are intended to convey the nature of the HRV by taste and health
982 interactions listed in Table 1. **(b)** The HRV endophenotype interacted with the
983 level of taste temptation faced during self-control challenges. To visualize this
984 result, the plot shows the response patterns from participants falling into the

highest (black square) and lowest (gray diamond) quartiles of total HRV. The x-axis represents the average taste difference level (i.e. SC difficulty) a participant faced during the dietary choice task. The estimated self-control success on the y-axis represents the model fit for discrete levels of the HRV by taste temptation interaction. Participants with higher HRV overcame even the largest taste temptations, whereas participants with low HRV who faced large taste temptations frequently failed to use self-control. Panel **(c)** analogously shows the interaction with the average difference in health: the higher the health difference between the two foods, the more health benefit could be gained by refusing the tastier item. The x-axis represents the average health difference level (i.e. potential SC benefit) a participant faced during the dietary choice task. The estimated self-control success on the y-axis represents the model fit for discrete levels of the HRV by health gain interaction. Participants with the lowest HRV rarely used self-control if potential health gains were small, whereas participants with the highest HRV engaged self-control at a relatively high level regardless of how much health benefit could be gained.

Figure 3. Heart-rate variability (HRV) is correlated with BOLD signal in the ventromedial prefrontal cortex (vmPFC). Panel **(a)**: Baseline HRV positively correlated with higher activity in Self-Control Challenge > No Challenge trials in the vmPFC ($p < 0.05$, small-volume corrected). The color bar represents small-volume corrected p-values. **(b)** Within this functional ROI, the relative taste representation (taste of the chosen minus taste of the non-chosen food) correlated negatively with individual HRV ($r = -0.42$, $p = 0.002$). **(c)** There was no significant correlation between HRV and the relative health value ($r = -0.12$, $p = 0.42$).

Tables

Table 1. Predictors of self-control success.

Fixed effects	Beta estimate	Standard Error of the Mean	T	p
Intercept	0.45483	0.04434	10.258	2.28e-12
Stress	-0.07869	0.06450	-1.220	0.23021
Tdiff	-0.02450	0.11721	-0.209	0.83555
Hdiff	0.35598	0.10108	3.522	0.00116
HRV	0.01239	0.03785	0.327	0.74524
RE	0.02995	0.03951	0.758	0.45326
Stress x Tdiff	-0.38367	0.11756	-3.264	0.00237
Stress x Hdiff	0.33003	0.11868	2.781	0.00848
HRV x Tdiff	0.30100	0.06253	4.814	2.51e-05
HRV x Hdiff	-0.20929	0.06429	-3.255	0.00242
RE x Tdiff	0.23935	0.07978	3.000	0.00481
RE x Hdiff	-0.17495	0.08761	-1.997	0.05323

Results from a general linear model of self-control success. Self-control success was computed as the mean number of trials in which participants chose the healthier, less tasty item in trials in which health and taste were not aligned (challenge trials). Resting heart-rate-variability (HRV) was defined as the standard deviation of all RR intervals over a three-minute period. The cognitive restraint in eating score (RE) was obtained from the Three Factor Eating Questionnaire (Pudel and Westenhöfer, 1989). The regressor, Stress, is a binary factor indicating that the participant underwent the stress manipulation. The average health (Hdiff) and taste difference (Tdiff) regressors represent the mean taste temptation and health gain that participants were faced with during the dietary choice task. All estimates are reported with their standard error of the mean (SEM).

Table 2. General linear model predicting total HRV (GLM-HRV).

Regressor	Beta estimate	Standard Error of the Mean	t	p
Intercept	189.41	31.17	6.08	< .001
# of Artifacts	5.07	1.49	3.41	0.0014
Mean Heart Rate	-1.17	0.47	-2.48	0.017
Trait Anxiety	-0.57	0.63	-0.91	0.37

Results from a general linear model with possible determinants of HRV (represented as untransformed values of SDNN in milliseconds): the number of artifacts corrected in the dataset and mean heart rate (after artifact correction by deletion). In order to assess whether trait anxiety explains additional variance beyond an increase in mean heart rate, we added a regressor with the trait anxiety score as measured by the Spielberger State-Trait-Anxiety Inventory, so that mean heart rate and trait anxiety compete for variance in the same model. When doing so, mean heart rate accounts for a decrease in HRV, but trait anxiety does not explain further variance. The results above hold when excluding the HRV outlier from this model.